

GENETICAL FEATURES OF FERNS AS CONTRASTED TO SEED PLANTS¹

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Many disjunct populations of plants are the result of the dispersal and germination of a single propagule; the seed in seed plants; the spore in homosporous ferns. Although both of these propagules are generally an aspect of sexual reproduction in these organisms, populations established from either a single spore or seed are genetically very distinct. Populations which differ genetically may be expected to exhibit different evolutionary prospects. This paper will attempt to elucidate these genetic differences and speculate upon their evolutionary prospects.

As Figure 1 shows, an angiosperm seed is a propagule which develops after meiosis and syngamy have occurred. This propagule contains the results of double fertilization; endosperm tissue and an embryo. Upon seed germination this embryo will develop into a mature sporophyte. The genotype of this sporophyte does not reflect its current isolation but rather is related to the breeding system of the parental sporophyte population. Thus it may be homozygous or very heterozygous.

In contrast, an homosporous fern spore is a propagule that develops after meiosis but prior to syngamy. In this case only a single haploid cell is dispersed and upon germination undergoes a series of mitotic cell divisions leading to the development of a haploid, generally autotrophic plant, the gametophyte. This organism is functionally hermaphroditic, simultaneously developing male and female gametangia at some point during its life. Self-fertilization (intragametophytic selfing) results in a single diploid cell, the zygote, which is completely homozygous. This homozygous cell undergoes mitotic cell divisions leading to the development of an embryo and eventually a mature sporophyte. Thus the establishment of a sporophyte from a single propagule in an homosporous fern results in a completely homozygous individual, whereas in a seed plant the sporophyte genotype may be heterozygous.

Because of the above genetic distinctions between a seed and a spore, the evolutionary future of disjunct populations of homosporous ferns and angiosperms might predictably be very different. The angiosperm sporophyte, if it is perennial and dioecious, may live long enough to encounter a sporophyte of the opposite sex, outcross, and form progeny. These resulting progeny in all likelihood would be heterozygous to some degree.

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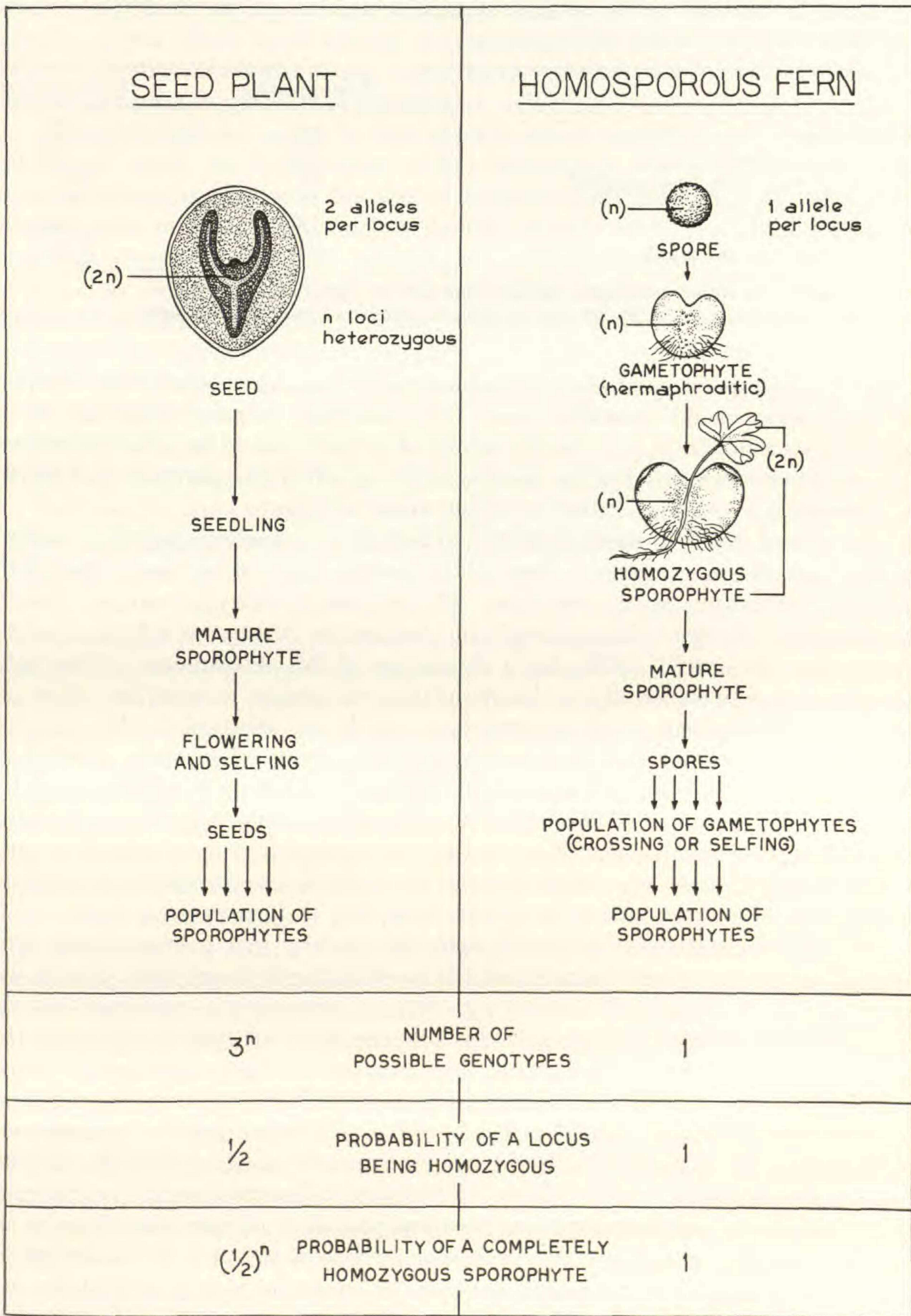


FIGURE 1. Genetic comparison of sporophyte populations established from a single seed or a single spore.

TABLE 1. Statistics of the gametic chromosome numbers of the Pteridophyta (only sexual taxa).^a

	Heterosporous	Homosporous
Overall mean	13	54
Mean base number ^b	12.7	37.5
Number of taxa with base number ^b	81	1027
Number of polyploid taxa	11	682
Percent polyploid	12%	40%
Total number of taxa tabulated	92	1709

^a Gametic chromosome numbers greater than 100 tabulated as 100.

^b Base numbers are usually the lowest gametic numbers reported in a genus.

If the angiosperm sporophyte is monoecious or bears hermaphroditic flowers, self-pollination would probably occur. The resulting progeny would be more homozygous than the parent, but the family of progeny would be a heterogeneous array of genotypes related to the number of loci at which the parental sporophyte was heterozygous. Figure 1 illustrates these relationships.

In contrast, the fern sporophyte established from a single propagule is necessarily completely homozygous. Thus all the genetic material has been exposed to selection in the homozygous condition. The progeny of this plant are completely homozygous whether intragametophytic mating or intergametophytic mating occurs (see Klekowski, 1970c, for a discussion of this terminology). The only possible source of variability in this population of progeny is mutation, since all normal recombinations result in genotypes which are identical to the parental sporophyte. Therefore, populations of homosporous ferns which were established by a single propagule will have only one allele per locus present, whereas populations of angiosperms established from a single propagule potentially could have two alleles per locus present. Since evolution is dependent upon inherited variability in populations, one might assume the evolutionary prospects of disjunct populations of angiosperms to be greater than that of homosporous ferns.

The above conclusions are based upon the premise that a homozygous fern sporophyte resulting from intragametophytic selfing will breed true; that is, its progeny will be genetically equivalent. Recent experiments conducted in my laboratory in Amherst indicate that this premise does not hold in all cases. In order to fully understand the nature and meaning of these experiments, some knowledge of the kind of genetic systems present in these organisms is necessary.

Klekowski and Baker (1966) pointed out the correlation that the homosporous pteridophyta are characterized by higher chromosome numbers than the heterosporous pteridophyta. Table 1 shows an analysis of the chromosome numbers in the homosporous and heterosporous pteridophyta. It is obvious that there is an excellent correlation between the utilization of polyploidy and the evolution of taxa in the homosporous pteridophyta. A model causally relating polyploidy and the capacity for intragametophytic selfing with its consequent homozygosity has been proposed to explain this correlation (Klekowski & Baker, 1966). A key point in this model is the idea that a plant genetic system must fulfill at least two roles; that is, the storage of genetic variability and its release. If intragameto-

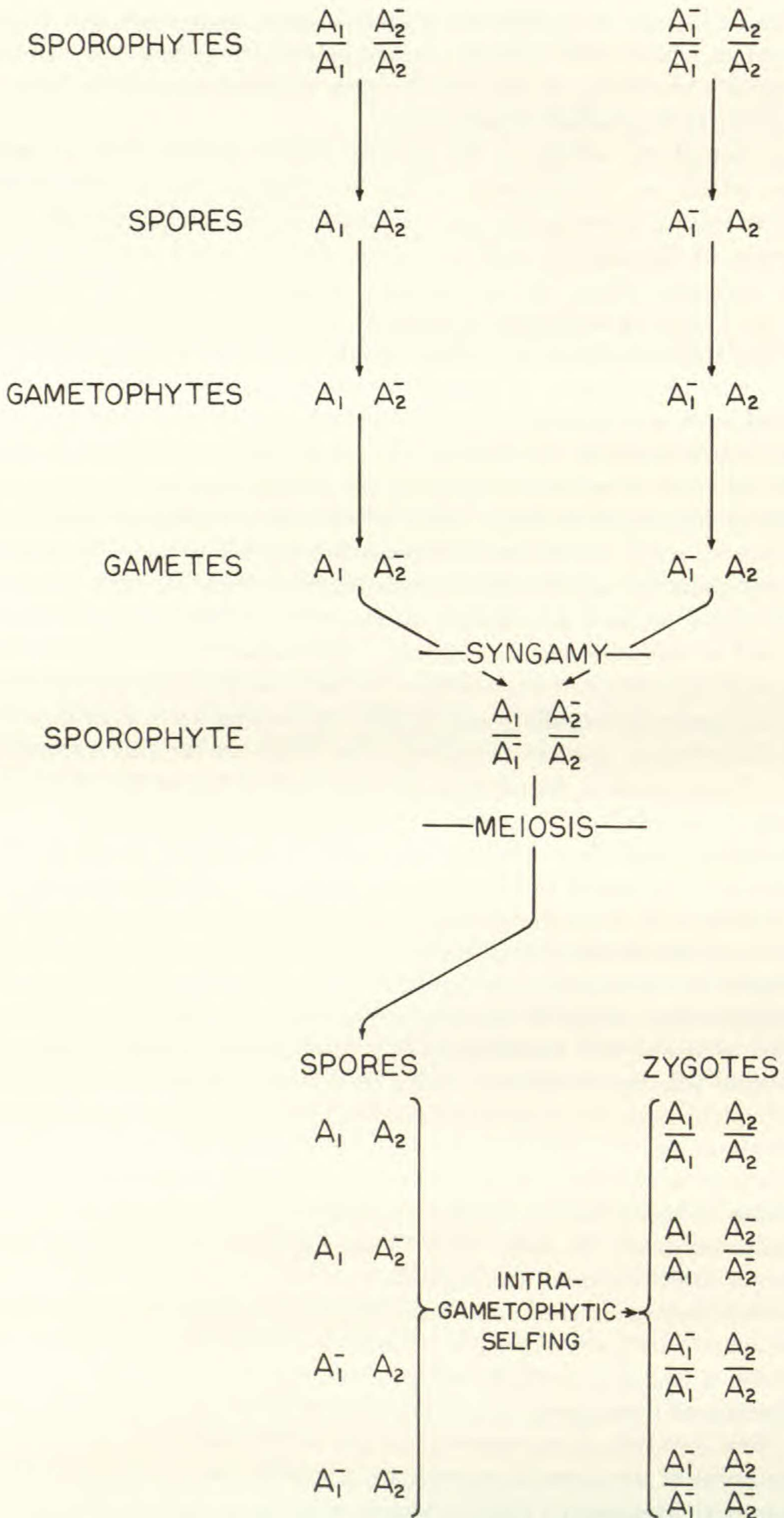
phytic selfing occurs in a diploid organism these two roles are negated. A genetic system which could tolerate intragametophytic selfing and still store and release genetic variability is one based upon unlinked duplicated loci. Such a genetic system is the product of polyploidy.

Intragametophytic selfing in this genetic system would result in sporophyte genotypes which are homozygous within homologous chromosomes but potentially heterozygous between the sets of homoeologous chromosomes. Given the phenomenon of dominance, such a genetic system could readily shelter from selection recessive alleles in sporophytes originating from intragametophytic selfing. As Figure 2 indicates, occasional hybridization between sporophytes followed by intragametophytic selfing would result in the generation of new genotypes and phenotypes. A polyploid genetic system, therefore, allows the storage and release of genetic variability in spite of intragametophytic selfing.

Recent experiments by my student, Mr. Leslie Hickok, and myself suggest the possibility of another means of releasing the genetic variability stored in duplicated loci in homosporous ferns. Sporophytes of *Ceratopteris pteridoides* and *C. thalictroides* were chosen as experimental material because of their ease of culture and short life cycles (Klekowski, 1970a). Both of these species are of polyploid origin, as the base number in the genus $x = 40$, is of polyploid origin. Genetic and cytogenetic studies utilizing x-ray induced and naturally occurring chromosomal aberrations (translocations and an inversion) support the hypothesis that the chromosomes regularly pair within homoeologous sets rather than with the same homologous partner at meiosis. The evidence for this interpretation of meiosis in *Ceratopteris* is based upon the cytological expression of chromosomal aberrations during meiosis in completely homozygous sporophytes.

Generalizing from these experiments with *Ceratopteris* to all of the homosporous ferns, it is possible to formulate an hypothesis whereby completely homozygous homosporous fern sporophytes can store and release genetic variability. It is hypothesized that homosporous ferns have evolved a genetic system based upon homoeologous heterozygosity and homoeologous recombination. Figure 3 graphically illustrates this means of recombination. It is assumed that the cytological mechanism whereby the homoeologous recombination occurs is via occasional homoeologous pairing at meiosis. Although bivalent formation at meiosis is the rule in polyploid ferns, it is hypothesized that these pairs are not limited to homologous chromosomes but involve members of homoeologous sets. This kind of meiotic pairing would allow the perpetuation of functionally duplicated loci. The phenomenon of diploidization would be retarded in a manner similar to a situation where multivalents are the rule. (See Ohno, 1970, and Mackey, 1970, for further discussion of diploidization in polyploids.)

Given homoeologous recombination, the genetic comparison of a seed and a spore presented in Figure 1 must be modified. Obviously some spore genotypes can establish a sporophyte which will produce genetically variable progeny. The main criterion of these spore genotypes is that they must be interlocus heterozygotes (Fig. 3). Whether a spore genotype fulfills this criterion is a reflection of the genotype of its parental sporophyte, which in turn is related to the taxon's mating system. Klekowski (1969b) has classified fern reproductive systems into



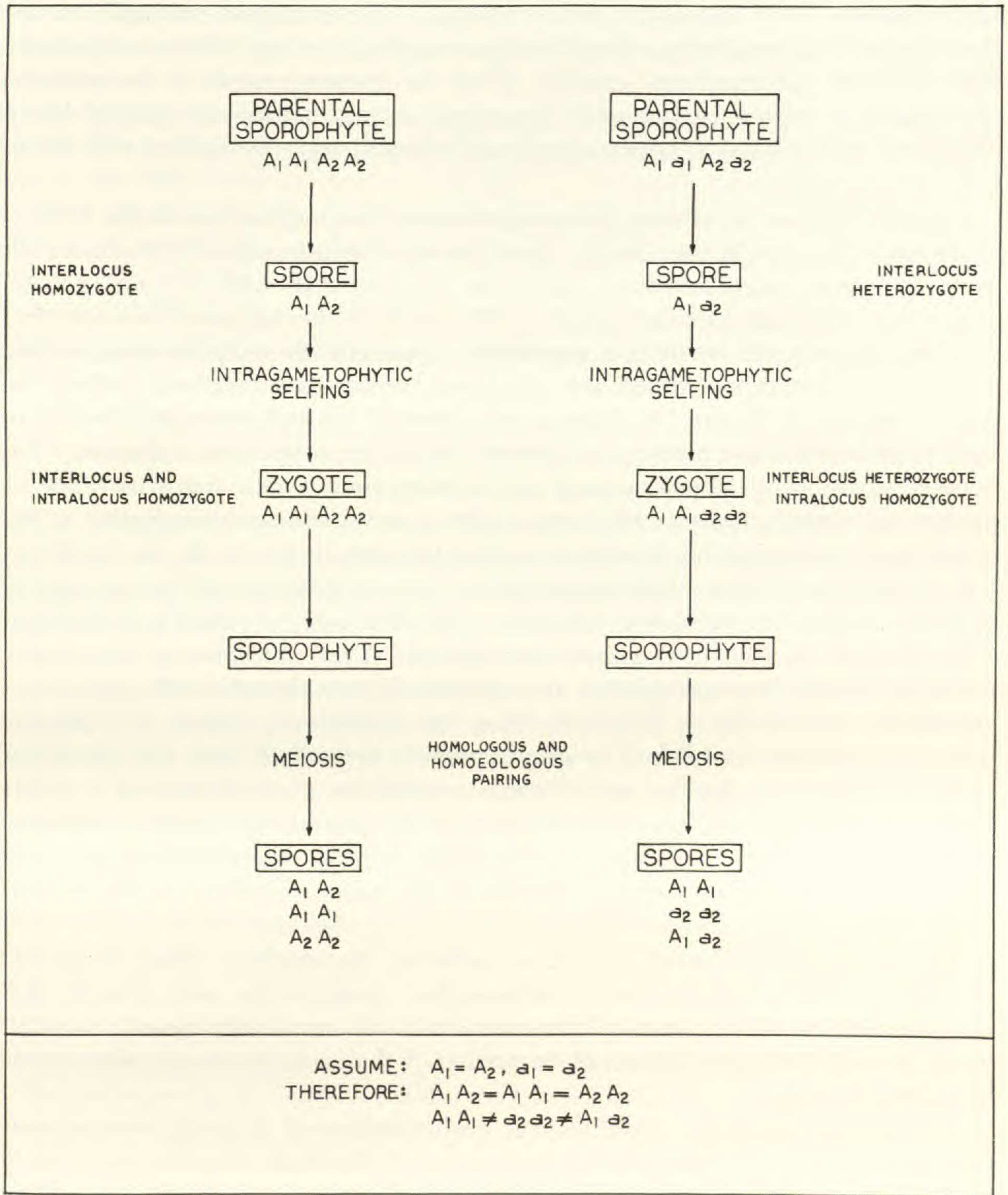


FIGURE 3. Homoeologous recombination model.

three categories; apogamy, intragametophytic mating, and intergametophytic mating. Only the latter two categories are sexual modes of reproduction. Taxa characterized by intragametophytic mating systems (fusion of gametes from the same gametophyte) generally have sporophyte genotypes with high levels of

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FIGURE 2. Storage of genetic heterozygosity in duplicated loci and its release via hybridization.

homozygosity (both intralocus and interlocus). Heterozygous sporophytes are more frequent in populations where intergametophytic mating (fusion of gametes from different gametophytes) occurs. Thus the mating system of the parental sporophyte is related to the spore genotype, intragametophytic mating being associated with interlocus homozygotes and intergametophytic mating with interlocus heterozygotes.

Spores which are interlocus heterozygotes have two implications in the biology of disjunct fern populations. Such a spore can develop into a gametophyte, which upon intragametophytic selfing, will form a sporophyte with unusual genetic properties. Although this sporophyte is the result of the fusion of two identical gametes, meiosis will result in a population of genetically variable spores. (See Figure 3). Thus spores which are interlocus heterozygotes will not follow the pattern outlined in Figure 1; a disjunct population of sporophytes established from such a spore will have a source of genetic variability other than mutation. The genetic relationship between a seed and a homosporous fern spore in Figure 1 applies only to situations in which the spore is an interlocus homozygote or the cytological mechanism for homologous recombination is absent. In the latter situation, spore genotypes which are interlocus heterozygotes are still advantageous from an evolutionary viewpoint. Genetic variability may be stored and sheltered from selection in such homozygous sporophytes. After a number of genetically different homozygous sporophytes are established, hybridization will release this variability, as is shown in Figure 2. Thus the evolutionary future of a disjunct population of ferns established by single spores is dependent upon the genotypes of those propagules. In the case where a population is established by a single spore, the genotype of that cell determines the sources of genetic variability available for subsequent evolution. If it is an interlocus homozygote, the main source of genetic variability in subsequent generations will be mutation, but where this propagule is an interlocus heterozygote, the sources of genetic variability will be recombination as well as mutation. In situations where a population has its origin in a number of independent spore entries and hybridization between new immigrants and indigenous individuals occurs, the genetic variability in the resultant population will be greater if the spore genotypes were interlocus heterozygotes.

Any discussion of the establishment and evolution of disjunct homosporous fern populations must start with an assessment of the kinds of spores most likely to establish sporophytes. Because of their size, there is no doubt that most fern spores can be dispersed great distances by the wind (Tryon, 1970). Lloyd (personal communication) reports that a *Nephrolepis* spore collected 2,000 feet above the ocean in the vicinity of Hawaii germinated readily and formed a normal gametophyte. A number of homosporous fern taxa have green spores with short viabilities in contrast to long viabilities in non-green spores such as *Nephrolepis* (Lloyd & Klekowski, 1970); therefore the dispersal capabilities of taxa with green spores might be expected to be less than non-green spores. However, since the majority of ferns have non-green spores, dispersal would not seem to be a great problem in the majority of these (Tryon, 1970).

Actual establishment of a disjunct population is dependent upon the estab-

lishment and survival of the gametophyte and the formation and maturation of a sporophyte. Since the subsequent evolutionary future of a disjunct population is dependent upon the genotype of this sporophyte, it is important to determine the probability for interlocus heterozygosity in this genotype. Two arguments will be advanced which suggest that the long distance establishment of such a genotype is less likely in homosporous ferns than an interlocus homozygote.

With reference to the establishment of a sporophyte from a single propagule, the length of the gametophyte generation is shortest in apogamous and intragametophytic mating systems and the longest in intergametophytic mating systems (Klekowski, 1969*b*; Whittier, 1970). Ferns with intergametophytic mating systems produce spores which have a higher probability of being interlocus heterozygotes. Since the mating system and the degree of interlocus heterozygosity are related, the ecology of the disjunct area has an influence on the kinds of spore genotypes which successfully establish sporophytes. Where ecological conditions are adverse to prolonged gametophyte growth, sporophytes with apogamous or intragametophytic mating systems will become established. Where ecological conditions are more conducive to prolonged gametophyte growth, taxa with apogamous, intragametophytic, and intergametophytic mating systems will be established. Figure 4 graphically illustrates this relationship between mating systems, ecology, and genetics in homosporous ferns.

Another factor decreasing the frequency of establishment of taxa with intergametophytic mating systems is the phenomenon of genetic load. Klekowski (1970*a, b*, 1971) has shown that many sporophytes in nature are heterozygous for recessive zygotic or early embryonic lethals. Such sporophytes produce many spore genotypes capable of developing into normal gametophytes which will not give rise to viable sporophytes when intragametophytic selfing occurs. The frequency of sporophytes heterozygous for such lethals might be expected to be higher in taxa with intergametophytic mating systems in comparison to taxa with intragametophytic mating systems. Thus in a given sample of spores entering a disjunct area, the gametophytes which have the capability of giving rise in isolation to a sporophyte will be predominantly from taxa with apogamous and intragametophytic mating systems. Another characteristic of genetic load in ferns is the phenomenon of "leaky lethality" (Klekowski, 1970*b*). Gametophyte genotypes vary in ability to form viable sporophytes. Experiments have shown (Klekowski, unpublished) that some gametophyte genotypes form sporophytes very readily whereas others do so only after repeated self-fertilizations (simple polyembryony). Gametophytes from heterozygous sporophytes exhibit "leaky lethality" to a greater degree than gametophytes from homozygous sporophytes. When a gametophyte exhibits this phenomenon of "leaky lethality," the formation of a viable sporophyte via intragametophytic selfing requires a longer period of gametophyte survival. Therefore the establishment of a disjunct population of a fern taxon with an intergametophytic mating is less probable on both ecological and genetic grounds.

Recent research on the genus *Lygodium* has revealed data which illustrate these points. *Lygodium volubile* forms sporophytes apogamously, and *L. heterodoxum* is a sexual taxon with an intergametophytic mating system. In the latter

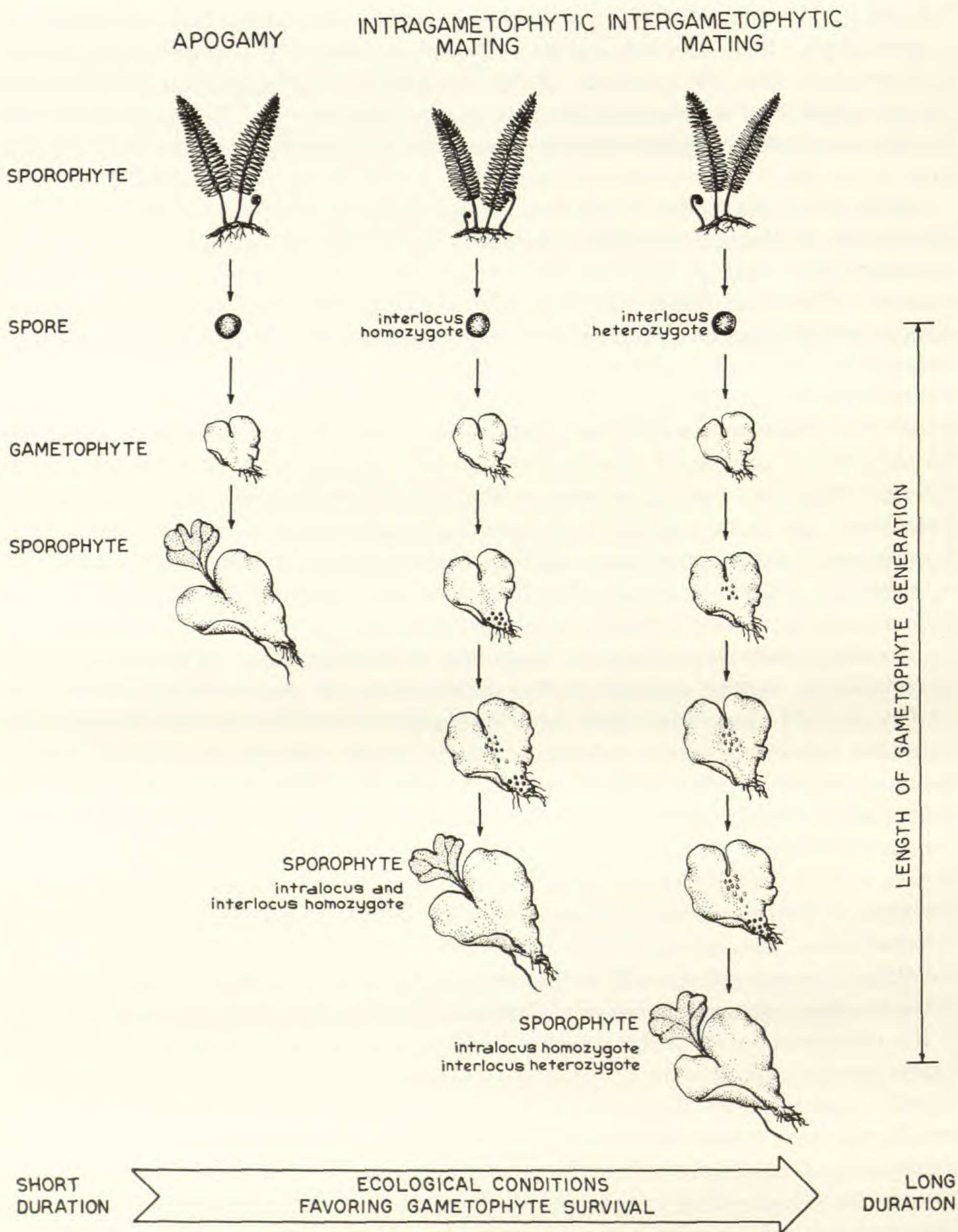


FIGURE 4. Relationship between reproductive systems, genetics, and ecology in homosporous ferns.

species, in composite cultures only male and female gametophytes are initially present, whereas if gametophytes are grown singly they are initially female and later become hermaphroditic (as do those in composite culture). These results are compatible with a mating system based upon antheridogen. Voeller (1971)

has documented the positive response of members of this genus to antheridogen B.

Under laboratory culture conditions (see Klekowski, 1969a, for description), *Lygodium volubile* forms sporophytes (first leaf) 30 days after spore sowing, whereas isolated gametophytes of *L. heterodoxum* begin to form sporophytes after 51 days from sowing. A sample of spores of *L. volubile* obtained from the Royal Botanic Gardens, Kew, was used in a breeding test; of the ten gametophytes isolated, all formed sporophytes that exhibited similar and apparently normal ontogeny. Thus in *L. volubile*, the apogamous taxon, all of the spore genotypes tested could function as a single propagule in sporophyte establishment.

Spores of *Lygodium heterodoxum* were obtained from a single sporophyte growing near Tela, Honduras. In the breeding test, 50 gametophytes were isolated and allowed to undergo intragametophytic selfing. Forty-eight of these gametophytes formed what appeared to be normal sporophytes. Two (4%) of the isolated gametophytes formed sporophytes which terminated their development prior to the elongation of the first root and leaf. Both gametophytes underwent simple polyembryony and each had a number of such inhibited embryos. Thus at least 4% of the spore genotypes could not function as a single propagule in the establishment of a sporophyte. Of the 48 homozygous sporophytes, 25 were transplanted into the greenhouse and allowed to undergo further development. Three months later these sporophytes were examined morphologically. Twenty-four of these plants exhibited abnormal patterns of growth. These abnormalities included differences in plant size, organ (leaf and root) development, and coloration with respect to chlorophyll development. These results are compatible with the hypothesis that the parental sporophyte was heterozygous for recessive detrimental alleles distributed throughout the genotype. During the ontogeny of these homozygous sporophytes, genes not expressed during the embryonic stages were "turned-on" as the plants grew older and more complex. As more of the genotype was utilized, new deleterious homozygous combinations became evident. Thus in *L. heterodoxum* approximately 4% of the spore genotypes could function as a single propagule and lead to the establishment of a viable sporophyte, whereas in the apomict *L. volubile* 100% of the spore genotypes tested fulfilled this criterion. Thus from both the genetic and ecological points of view the apogamous species (*L. volubile*) would establish disjunct populations more readily than the outbreeding species (*L. heterodoxum*). In contrast, disjunct populations of the latter species would more readily evolve into endemic taxa than the former.

Given these ecological and genetic relationships, the comparison of the evolutionary prospects of disjunct populations in homosporous ferns and seed plants reveals some novel differences. Without doubt the dispersibility of spores is greater than seeds. This has led to the hypothesis that the principal limiting factor in the evolution of island endemics in ferns is the regressive effects of gene flow from source areas into these disjunct areas (Tryon, 1970). The foregoing discussions have indicated that because of the peculiar interactions between genetics and ecology in homosporous ferns, a hypothesis can be formulated that in certain disjunct populations the principal limiting factor in the evolution of endemic taxa is the genetically depauperate nature of these populations.

There is a limited amount of experimental evidence to support this latter

TABLE 2. Genetic load studies in Galapagos and Hawaiian *Pteridium*.

GALAPAGOS ISLANDS				HAWAIIAN ISLANDS			
Spore Collection	Isolates	Sporophytes	%	Spore Collection	Isolates	Sporophytes	%
G1	20	20	100	4672	49	46	94
G6	50	50	100	4677	50	46	92
G3	49	45	92	BL-2	45	40	89
G7	49	45	92	4671	49	37	76
G5	49	43	88	4657	46	31	67
G8	48	39	81	4375	40	13	33
				4666	50	14	28

hypothesis. Contrasting the degree of endemism in the floras of the Hawaiian and Galapagos Islands reveals some interesting relationships. The Hawaiian Islands are more isolated geographically from continental source areas than the Galapagos Islands. Carlquist (1967) has indicated that in the Hawaiian flora 94.4% of the angiosperm species are endemic in contrast to 60–70% of the fern species. The 1400–2000 contemporary species and varieties of angiosperms probably evolved from 168 immigrants (Carlquist, 1967), whereas 142 contemporary species and varieties of ferns probably evolved from 97 immigrants (Wagner, personal communication). In contrast, in the Galapagos flora, of the 59 taxa of ferns present, 5% are endemic, whereas of the 531 seed plants, 44.7% are endemic (Wiggins, 1966). These data appear interpretable upon the basis that the differences in fern endemism are related to the differences in geographical isolation of these two groups of islands. One might assume that greater geographical isolation results in greater genetic isolation and that in the ferns this is reflected in the greater degree of endemism in the Hawaiian Islands as contrasted to the Galapagos Islands.

Recent studies on the genetics of the cosmopolitan fern species *Pteridium aquilinum* (Klekowski, 1972) indicates that this interpretation may be too simple. Spore samples from individual sporophytes in both island groups were screened for embryonic recessive lethals. A gametophyte culture was generated and populations of paired and isolated gametophytes were established from the spores of each sporophyte sampled. If the parental sporophyte were heterozygous for recessive lethals, a portion of the hermaphroditic gametophytes in both populations failed to form sporophytes. Evidence that the failure of hermaphroditic gametophytes to form sporophytes is due to genetic causes is shown by the consistently higher frequencies of sporophytes in the paired populations. Table 2 compares the response of Hawaiian and Galapagos spore samples. From the isolation hypothesis one might predict the Hawaiian plants to show greater genetic uniformity and less heterozygosity for lethals than the Galapagos plants. Actually the data indicate the converse. The Galapagos *Pteridium* is more homogeneous and exhibits less heterozygosity for lethals than the Hawaiian *Pteridium*. In the former, 9% of the spore genotypes tested evidenced the presence of recessive sporophytic lethals whereas in the latter, 31% of the spore genotypes exhibited this phenomenon. The Hawaiian *Pteridium* populations seem more heterozygous than the Galapagos *Pteridium* populations. This is correlated with the fact that the Hawaiian *Pterid-*

ium has evolved into an endemic taxon (Tryon, 1941), whereas the Galapagos *Pteridium* is similar taxonomically to the South American form. Thus in *Pteridium*, evolution of an endemic taxon is correlated with the presence of greater genetic variability in the disjunct population. Conversely, the lack of evolution may be attributed to the genetically depauperate nature of the disjunct Galapagos populations rather than gene flow from neighboring South America.

To explain this paradoxical relationship between apparent geographical isolation and increased genetic heterozygosity, the ecology of these two groups of islands must be considered. Contrasting the Hawaiian Islands to the Galapagos Islands, the former would probably offer more habitats for prolonged gametophyte growth and survival than the latter. Such a situation would allow the establishment of taxa with intergametophytic mating systems and, with reference to *Pteridium*, sporophytes which are interlocus heterozygotes. In the more xeric Galapagos Islands one would expect a preponderance of taxa which are apogamous or have intragametophytic mating systems to become established. With reference to the Galapagos *Pteridium*, gametophytes originating from spores of inbred mainland sporophytes would form sporophytes more readily, and these probably would be interlocus homozygotes (see previous discussion on leaky lethality and ecology).

This relationship is supported by recent research on the Hawaiian fern genus *Sadleria*. This genus is endemic to Hawaii and comprises four species. Holbrook (1971) has found that three of the four species have intergametophytic mating systems and that heterozygosity for recessive sporophytic lethals is present in the populations. In this case endemism is correlated with the presence of intergametophytic mating and heterozygosity. Thus the differences between the frequency of fern endemics on the Hawaiian and the Galapagos Islands are explicable in terms of the differences in the ecologies of these two groups of islands. In all the above discussions the differences in ages of these two groups of islands has not been considered, it has been assumed that both groups of islands have been in existence sufficient periods of time to discount their age differences.

CONCLUSIONS

The high dispersability of the spores and the determination of the zygote genotype after migration are pivotal characteristics in any discussions of the genetics and evolution of disjunct fern populations. An independent consideration of either characteristic can result in two distinct, and somewhat antithetic, hypotheses concerning the nature of evolutionary processes in disjunct fern populations. In his study of island fern floras, Tryon (1970), considered gene flow from source areas (because of the ease of spore dispersability) to be an important agent in retarding the evolution of island fern endemics. For convenience this will be called the "reproductive isolation hypothesis." In this communication the author has considered the second characteristic (determination of the zygote genotype after migration) at great length. Because of the relationship of the fern mating system to its ecology and genetics, it has been argued that the primary phenomenon retarding the evolution of fern endemics is the absence of inherited variability in disjunct populations. For convenience this is called the "genetic depauperization hypothesis."

The relationship between these two hypotheses is illustrated by the following example. Assume an island is populated by a number of fern species, a few of which are endemic. The acceptance of either hypothesis for this hypothetical situation will result in a separate and distinct set of predictions concerning the biology of the endemic and non-endemic ferns present on the island. Assuming the validity of the "reproductive isolation hypothesis," one would expect the levels of heterozygosity in the populations of non-endemics to approximate those of their respective source areas, whereas the endemics would be characterized by lower levels of heterozygosity than populations of closely related taxa in source areas. One also would predict the absence of any correlation between mating system and endemism.

The "genetic depauperization hypothesis" would predict lower levels of heterozygosity in the non-endemic taxa in comparison to populations in their respective source areas. The populations of the endemics would be characterized by higher levels of heterozygosity than those of the non-endemics. The degree of heterozygosity of the endemics would approach that of populations of related taxa in source areas. Intergametophytic mating systems would predominate in endemic taxa whereas non-endemics could be apogamous or have either intergametophytic or intragametophytic mating systems.

Both the "reproductive isolation hypothesis" and the "genetic depauperization hypothesis" represent extreme interpretations based upon very restricted amounts of real data. The usefulness of these hypotheses lies in the predictions which can be formulated because of their extreme positions. As data are gathered on the taxonomy, gametophyte biology and genetics of island fern floras and other disjunct populations of ferns, these predictions can be tested. The outcome of these researches probably will indicate that both of these views are too simplistic and that the biology of disjunct fern populations represents an integration of both hypotheses with as yet unsuspected parameters of fern biology.

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